Received: 25 September 2020 | Accepted: 9 April 2021

DOI: 10.1111/1365-2664.13900

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality

Sebastian Fiedler[1,2,3] | José A. F. Monteiro[1,2,4] | Kristin B. Hulvey[5] | Rachel J. Standish[6] | Michael P. Perring[7,8,9] | Britta Tietjen[1,2]

[1]Freie Universität Berlin, Theoretical Ecology, Institute of Biology, Berlin, Germany; [2]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany; [3]Department of Ecological Modelling, University Bayreuth, Bayreuth, Germany; [4]Statistical Office Basel-Stadt, Basel, Switzerland; [5]Working Lands Conservation, Logan, UT, USA; [6]Environmental and Conservation Sciences, Murdoch University, Murdoch, WA, Australia; [7]Forest & Nature Lab, Ghent University, Gontrode-Melle, Belgium; [8]Ecosystem Restoration and Intervention Ecology Research Group, School of Biological Sciences, The University of Western Australia, Crawley, WA, Australia and [9]UKCEH (UK Centre for Ecology and Hydrology), Environment Centre Wales, Bangor, UK

Correspondence
Sebastian Fiedler
Email: sebastian.fiedler@online.de

Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: TI 824/3-1; Deutscher Akademischer Austauschdienst; European Research Council, Grant/Award Number: 614839; University Alliance for Sustainability; Australian Research Council

Handling Editor: Lars Brudvig

Abstract

1. Ecological restoration increasingly aims at improving ecosystem multifunctionality and making landscapes resilient to future threats, especially in biodiversity hotspots such as Mediterranean-type ecosystems. Plants and their traits play a major role in the functioning of an ecosystem. Therefore, successful restoration towards long-term multifunctionality requires a fundamental mechanistic understanding of this link under changing climate. An integrated approach of empirical research and simulation modelling with a focus on plant traits can allow this understanding.
2. Based on empirical data from a large-scale restoration project in a Mediterranean-type ecosystem in Western Australia, we developed and validated the spatially explicit simulation model *Modelling Ecosystem Functions and Services based on Traits* (ModEST), which calculates coupled dynamics of nutrients, water and individual plants characterised by functional traits. We then simulated all possible combinations of eight plant species with different levels of diversity to assess the role of plant diversity and traits on multifunctionality, the provision of six ecosystem functions that can be linked to ecosystem services, as well as trade-offs and synergies among the functions under current and future climatic conditions.
3. Our results show that multifunctionality cannot fully be achieved because of trade-offs among functions that are attributable to sets of traits that affect functions differently. Our measure of multifunctionality was increased by higher levels of planted species richness under current, but not future climatic conditions. In contrast, single functions were differently impacted by increased plant diversity and thus the choice and weighting of these functions affected multifunctionality. In addition, we found that trade-offs and synergies among functions shifted with climate change due to different direct and indirect (mediated via community trait changes) effects of climate change on functions.

4. *Synthesis and application*. With our simulation model *Modelling Ecosystem Functions and Services based on Traits* (ModEST), we show that restoration towards multifunctionality might be challenging not only under current conditions but also in the long-term. However, once ModEST is parameterised and validated for a specific restoration site, managers can assess which target goals can be achieved given the set of available plant species and site-specific conditions. It can also highlight which species combinations can best achieve long-term improved multifunctionality due to their trait diversity.

KEYWORDS

biodiversity, climate change, ecosystem services, functional traits, Mediterranean-type ecosystem, multifunctionality, plant traits, simulation model

1 | INTRODUCTION

Global change is contributing to a decline in biodiversity and ecosystem functions, which can underpin some of the ecosystem services that people rely on for their well-being (IPBES, 2019). Degradation associated with past change, and concern for the future supply of multiple ecosystem services is particularly apparent in Mediterranean-type ecosystems where remarkably high diversity is threatened by multiple environmental changes (Cowling et al., 1996; Sala, 2000). Reverting the consequences of ecosystem degradation may necessitate the process of ecological restoration which can target different goals such as the recovery of historic conditions or functional integrity of an ecosystem (Gann et al., 2019). In socio-ecological systems such as Mediterranean-type ecosystems, restoration may seek to achieve a long-term and simultaneous delivery of multiple ecosystem functions and services (Shackelford et al., 2013).

Managing landscapes for multiple functions or services simultaneously requires a direct comparison of their delivery (e.g. Byrnes et al., 2014; Manning et al., 2018). With increasing evidence that higher levels of ecosystem functions and services are associated with greater species numbers (e.g. Cardinale et al., 2012; Soliveres et al., 2016), the traditional focus of restoration on plant biodiversity appears justified (Perring et al., 2015). Enhanced biodiversity, however, does not necessarily increase the simultaneous and resilient provision of multiple ecosystem functions and services (Gamfeldt & Roger, 2017; Meyer et al., 2018; van der Plas, Manning, Allan, et al., 2016) and the effect of global change on species and ecosystem functioning remains unclear (Giling et al., 2019).

In an attempt to further the understanding of biodiversity's role within ecosystems, restoration ecology has more recently made use of the functional trait concept allowing selection of plant species based on their response and effect traits (Laughlin, 2014; Lavorel & Garnier, 2002). A focus on effect traits, which have been found to be linked to many ecosystem functions (Lavorel & Garnier, 2002), allows for a better comparison across individuals and plant species. Individual environmental factors affect individual functions/services via plant traits (e.g. Lavorel & Garnier, 2002; Suding et al., 2008). However, plant traits are not always linked to single functions. Instead, multiple traits can affect one function, and multiple functions can be affected by a single trait (de Bello et al., 2010), and multiple functions can influence a single ecosystem service (Fu et al., 2013). Such relationships are particularly important if traits positively affect one function while at the same time negatively impacting another one—so-called trade-offs (Bennett et al., 2009). Knowing the trade-offs as well as synergies among plant traits and functions is therefore important for selecting plant species based on their traits to simultaneously improve multiple functions/services.

In addition, multiple environmental change factors that directly, or indirectly (via altered plant trait distributions), affect ecosystem functions can have non-additive effects (e.g. Luo et al., 2008). Restoration strategies based on individually studied effects could therefore be problematic when trying to achieve a long-term supply of functions and services. Furthermore, traits within a plant community may be affected differently by environmental factors, and therefore the provision of trait-mediated ecosystem functions may be affected differently as well. Consequently, trade-offs among ecosystem functions/services observed under current environmental conditions might not be the same under future conditions.

To improve understanding and allow more informed restoration, Fiedler et al. (2018) suggested an integrated approach that focuses on plant traits and combines the strengths of empirical and simulation modelling studies. Empirical approaches can support modelling approaches with essential data, while simulation models can extend empirical approaches by allowing assessment of the multi-layered relationship between multiple environmental factors, plant traits and ecosystem functions/services over larger temporal and spatial scales. Current trait-based simulation models provide a good basis for this approach (e.g. Esther et al., 2011; Fyllas & Troumbis, 2009; Schaphoff et al., 2018). However, to be able to support restoration towards multifunctional and resilient ecosystems, simulation models need to be combined and extended to meet the following criteria: (a) coupled processes for soil water, nutrient and plants as well as the respective feedbacks allowing to mechanistically study the impact of global change on ecosystem functioning (Fiedler et al., 2018), (b)

consideration of individual interactions (e.g. facilitation and competition) as well as spatial heterogeneity relevant for applied restoration projects implemented on smaller spatial scales (DeAngelis & Grimm, 2014; Pacala & Deutschman, 1995) and (c) a thorough validation of model outcomes against field data to make simulation models applicable for restoration.

Based on existing model tools and a restoration experiment in a Mediterranean-type ecosystem in SW Australia (Perring et al., 2012), we therefore developed and validated the individual- and trait-based simulation model Modelling Ecosystem Functions and Services based on Traits (ModEST). ModEST links water, nitrogen and plant processes dependent on climatic and other environmental conditions and exhibits enough generality to transfer findings beyond this specific study site. In our model analysis, we focused on six biophysical ecosystem functions that might be important when restoring degraded Mediterranean-type ecosystems (i.e. groundwater recharge, ecosystem water use efficiency, ecosystem nitrogen use efficiency, litter quality, plant and soil carbon increments) with the goal to improve them simultaneously under current and future climatic conditions. Even though we focused on these specific functions, they can be linked to several provisioning and regulating ecosystem services, such as water supply, wood production, nutrient cycling and carbon sequestration which might be of greater interest to particular stakeholders.

In this study, we approached the following specific research questions:

1. What is the role of planted species richness under current and future conditions on multifunctionality, and the provision of the six separate ecosystem functions?
2. How will environmental changes affect trade-offs and synergies among the ecosystem functions of simulated plant communities?
3. What sets of plant traits and correlations among them in the simulated plant communities provide our focal ecosystem functions under current and future conditions?

With this approach we highlight that ModEST can be used for supporting long-term restoration if enhancement of ecosystem functions/services via planting woody plants under changing climate is the general goal. We further discuss how ModEST can be used for different environmental contexts and restoration targets.

2 | MATERIALS AND METHODS

2.1 | Model description

We developed a spatially explicit model, ModEST which simulates the coupled daily dynamics of nutrients, water and individual woody plants (Figure 1), from which different ecosystem functions and services can be estimated (Fiedler et al., 2020). The model landscape is subdivided into grid cells (5 × 5 m^2), two soil layers and individual plants characterised by coordinates within the landscape. The model runs for different environmental settings concerning soil texture, climatic conditions, topography, initial plant composition and their traits, with full descriptions given in Appendices S1 and S2. In the following, we briefly describe the three coupled modules of ModEST.

The nutrient module is based on processes for simulating soil nitrogen and soil carbon described in the model SWAT (Kemanian et al., 2011). Daily dynamics of soil organic matter (SOM), nitrate and ammonium in two soil layers are driven by *nitrogen deposition* from the atmosphere, *decomposition* and *humification* of plants' residue to SOM, *immobilisation*, *mineralisation* to ammonium, *nitrification* to

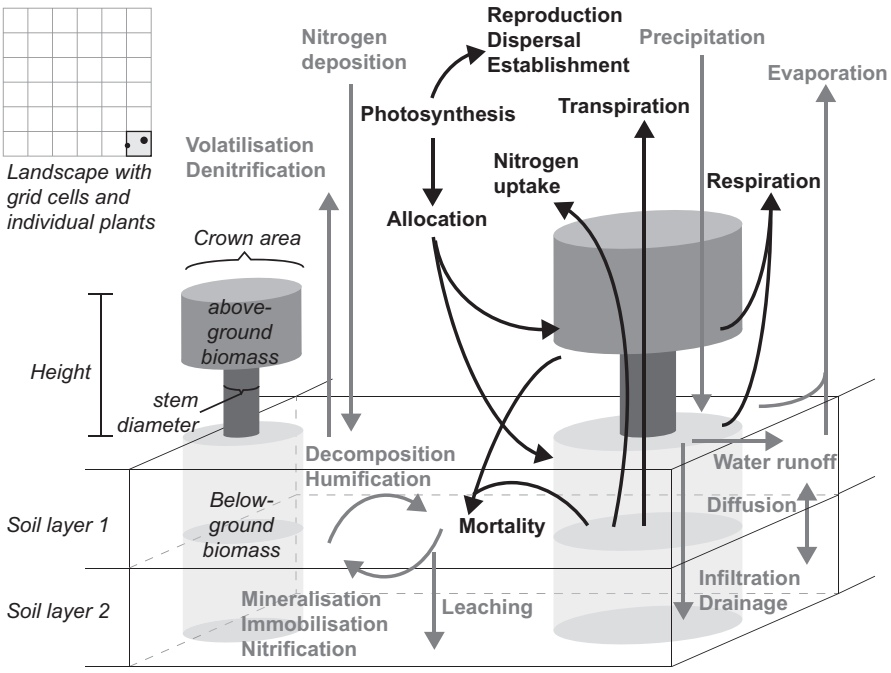

FIGURE 1 Structure (*italic*) and processes (bold) of Modelling Ecosystem Functions and Services based on Traits. The modelled landscape is subdivided into grid cells consisting of two soil layers as well as individual woody plants that are characterised by above- and below-ground features and are continuously distributed over the landscape. Coupled processes are calculated, that is hydrological and nutrient processes for each grid cell and soil layer (bold grey) as well as plant processes for each individual plant (bold black) depending on the resources of its covering grid cell

nitrate as well as nutrient losses through *volatilisation*, *denitrification* and *leaching*.

We based the hydrological module on the approach of Tietjen et al. (2009), who simulated surface water and soil moisture in two soil layers. Daily water dynamics are driven by *precipitation*, *lateral water redistribution of surface water* (*affected by vegetation cover*), *infiltration*, *vertical fluxes* and water losses via *evaporation* and *transpiration*. For ModEST, we adopted these processes with the exception of transpiration which we implemented after LPJ and LPJml (Schaphoff et al., 2018; Sitch et al., 2003) to better account for stomatal conductance (see description of the transpiration process in Appendix S1) as well as infiltration which is now affected by the proportion of plant roots in the two soil layers. Evaporation, lateral surface water distribution and infiltration are affected by vegetation simulated in the plant module.

The plant module is mainly based on LPJ and LPJmL (Schaphoff et al., 2018; Sitch et al., 2003; Smith et al., 2014) and local processes as described for an individual-based plant model by May et al. (2009). The module simulates the life cycle of individual woody plants placed in the landscape, their dynamic below- and aboveground carbon and nitrogen pools as well as structural components (e.g. plant height, crown area) based on plant traits and abiotic conditions. We adopted—with some changes—the plant processes *photosynthesis*, *transpiration*, *respiration*, *reproduction* and *allocation* after Sitch et al. (2003) and Schaphoff et al. (2018), *nitrogen uptake* after Smith et al. (2014), as well as *dispersal and establishment* after May et al. (2009). We added a simple *plant mortality* process based on annual plant growth and a species-specific growth threshold below which the individual plant dies. Given these adaptations, we fully describe this module in Appendix S1.

2.2 | Model parameterisation and validation

We parameterised and validated ModEST based on the settings of the Ridgefield experiment, a large-scale restoration experiment situated in the wheatbelt of SW Australia on former agricultural land (Perring et al., 2012). The experiment is located in a Mediterranean-climate region (32°29′S 116°58′E, elevation 350 m a.s.l.) with mean annual rainfall of 453 mm (2013–2019) and precipitation mainly during winter. The average maximum daily temperature in January is 30.7°C and the average minimum daily temperature in August is 7.6°C.

We parameterised morphological, reproductive and physiological traits (Table S2.1) of eight evergreen shrub and tree species (*Eucalyptus loxophleba* ssp. *loxophleba*, *E. astringens*, *Acacia acuminata*, *A. microbotrya*, *Banksia sessilis*, *Hakea lissocarpha*, *Calothamnus quadrifidus*, *Callistemon phoeniceus*). Species were selected because they had different nutrient acquisition strategies, growth forms and sizes, rooting depths, flower colours and bloom times, all properties that we expected to influence ecosystem functions, including some not modelled here, for example, pollination (Perring et al., 2012). We used the most prevalent soil type (loamy sand, Table S2.2) in the experiment (see Appendix S2 for full description of model parameterisation).

For model validation, we checked the outcome of the parameterised model against measurements from Ridgefield plots (see Appendix S2 for model settings). We quantitatively compared simulated and observed dynamics using Spearman's rank correlation *r* and the root mean square error *RMSE* (Figure S2.2). Simulated above-ground alive biomass, mean plant height and surviving individual counts agreed well with the measured data [i.e. significant ($p < 0.01$) correlations, low RMSE]. Exceptions were the biomass dynamic of *B. sessilis* and the population dynamics of *C. quadrifidus* and *C. phoeniceus*, where correlations were insignificant. However, RMSE for these cases remained low (RMSE < 1.0), indicating only small deviances between simulated and measured dynamics, and suggesting reasonable model behaviour.

2.3 | Simulation experiments

We simulated a full-factorial design of plant species combinations using the eight species included in the Ridgefield study (and thus simulating plant assemblages beyond those planted at Ridgefield) to assess ecosystem functioning under current and future climatic conditions. The flat modelled landscape (50 × 50 m^2) contained a homogenous soil texture of loamy sand, with initial soil moisture (=0.15 m^3/m^3), ammonium (=2.35 mg/kg) and nitrate (=9.92 mg/kg) set to the mean measured values across all Ridgefield plots with soil texture loamy sand. Each scenario was repeated 10 times to account for stochasticity in the initialisation of plant individuals (see *Species richness scenarios*), weather input (see Section 2.3.2) and the dispersal process (see model description in Appendix S1).

2.3.1 | Species richness scenarios

All possible combinations of the eight woody plant species used in the Ridgefield experiment were simulated leading to 255 different plant species compositions. Using this design, communities covered a wide range of different plant trait combinations, and species richness varied from monocultures to eight-species mixtures with increasing functional diversity (Figure S4.1). For each simulation, 500 one-year-old individuals with the same or a similar initial individual number of each present species were randomly positioned in the landscape with 2 m distance to neighbouring individuals. Initial plant heights were randomly drawn from a species-specific normal distribution that was obtained from height distributions of the 1-year planted individuals in the Ridgefield experiment (Figure S3.1).

2.3.2 | Climate change scenarios

For current climatic conditions, we used corrected daily precipitation, minimum and maximum air temperature and solar radiation data

from 1990 to 2018 from the weather station in Pingelly (32°31′S 117°04′E, 297 m a.s.l.) about 12 km away from our study site (Bureau of Meteorology, 2019, Appendix S3.1). Atmospheric CO_2 was set to 400 ppm.

For assessing impacts of climate change, we obtained the anomalies for future conditions (2080–2099) compared to past conditions (1986–2005) separately for each season based on the four climate projection Representative Concentration Pathways (RCPs) for SW Australia (Hope et al., 2015). We added the median reported trend between past and future climate from different global climate model simulations to the current weather data from Pingelly to generate realistic time series of future weather data. Atmospheric CO_2 was set according to IPCC (2014).

For each model repetition, we randomly selected annual weather data from the current or future weather dataset, given the climate scenario, to get 50 years of weather time-series input data.

For better clarity, we focused on the most extreme climate projection RCP 8.5 with an increase in mean annual air temperature of 3.4°C and a decrease in mean annual precipitation of 16% (Table S3.1; Figure S3.2). Across the different RCPs, ecosystem functioning exhibited qualitatively similar patterns (Figure S4.2).

2.3.3 | Evaluation of simulation outcomes

To assess the provision of, and trade-offs and synergies among, ecosystem functions, we determined the supply of six functions related to water, nitrogen and carbon (Table 1), that is, groundwater recharge (GWR), ecosystem water use efficiency (EWU), ecosystem nitrogen use efficiency (ENU), ecosystem litter quality (ELQ), total plant (PCI) and soil carbon increments (SCI). We selected these functions as they may be important to consider when restoring water- and nutrient-limited Mediterranean-type ecosystems (Luo et al., 2020). These functions can be linked to several provisioning and regulating ecosystem services, such as water supply, wood production, nutrient cycling and carbon sequestration.

For measuring multifunctionality, we first standardised each ecosystem function value based on the maximum and minimum value found for the same function. As these extreme values varied across the climate scenarios, we assessed how the context (current vs. future climate) affected the standardisation of the functions. Therefore, we standardised each function value based on the extreme values found either within, or across, climate scenarios. We then calculated multifunctionality for a given simulation as the mean of these standardised single function values, thus giving two values per simulation, that is, within a climate scenario, or across climate scenarios. The multifunctionality measure follows the approach by van der Plas, Manning, Allan, et al. (2016), however, without comparing functioning against a desired minimal threshold which significantly affects the outcome (see Figure S4.3, left panel). In the absence of other information, we weighted all ecosystem functions equally, therefore giving them equal importance within our measure of multifunctionality. We assessed the sensitivity of our outcomes by using different measures of multifunctionality (see Figure S4.3, right panel) or by different inclusions or weightings of our focal functions (see Figure S4.4).

We calculated the community weighted mean (CWM) for selected traits (Table 2) to evaluate the plant trait distribution. These traits are measurable in the field and therefore applicable for ecosystem restoration.

We evaluated model outcomes between 40 and 50 years given attainment of dynamic equilibrium in total plant species cover after 40 years (Figure S3.3). All relationships were analysed by a Spearman's rank correlation.

3 | RESULTS

3.1 | Planted species richness effects on ecosystem functioning

Ecosystem multifunctionality, with individual functions standardised within a given climate scenario, increased with planted and realised richness under current climate conditions, but decreased under future conditions (Figure 2a, left; see also Figure S4.5).

TABLE 1 Ecosystem functions assessed in this study, how they are measured from Modelling Ecosystem Functions and Services based on Traits, and their potential linkages to ecosystem services

Ecosystem function	Model output	Unit	Potential link to ecosystem service
Groundwater recharge (GWR)	Annual deep (>2 m in soil depth) soil water drainage per m^2	mm/year	Water supply
Ecosystem water use efficiency (EWU)	Annual net primary productivity (NPP) per m^2/Annual precipitation per m^2	g L^{-1} $year^{-1}$	Water supply, Wood production
Ecosystem nitrogen use efficiency (ENU)	Annual NPP per m^2/Annual mean soil avail. nitrogen per m^3	kgNPP m^{-2} kgN^{-1} m^{-3}	Nutrient cycling, Wood production
Ecosystem litter quality (ELQ)	Annual nitrogen per m^2/Annual carbon per m^2 from plant's residue	gN $year^{-1}$ kgC^{-1} $year^{-1}$	Nutrient cycling
Total plant carbon increment (PCI)	Annual plant carbon increment	kg m^{-2} $year^{-1}$	Carbon sequestration
Total soil carbon increment (SCI)	Annual soil carbon increment	t m^{-2} $year^{-1}$	Carbon sequestration

TABLE 2 Focal plant traits assessed in this study. Trait values for the plant species used in this study are shown in Table S2.1

Abbreviation	Description of plant trait	Unit
SLA	Specific leaf area	m^2/kg
rootL1	Fraction of total root mass between 0 and 50 cm of the soil horizon	—
seedMass	Seed mass	mg
WP	Relative water content at wilting point for soil texture loamy sand	—
CNleaf	Carbon to nitrogen ratio in the leaves	—
LM/RM	Allometric constant describing optimal ratio of leaf to root mass	—
meanDisp	Mean dispersal distance of seeds	m
maxCA	Maximum crown area	m^2
WD	Wood density	kgC/m^3

However, when considering minimum and maximum value per function across climate scenarios, current multifunctionality decreased with greater richness (Figure 2a, right). In addition, the relationship between multifunctionality and planted richness depended not only on the calculation of multifunctionality (Figure S4.3) but also on the choice and weighting of ecosystem functions (Figure S4.4).

In the latter, our measure of multifunctionality was not always enhanced by increased planted species richness since single ecosystem functions increased or decreased with planted species richness under current conditions (Figure 2b). Climate change strengthened this pattern and increased variability for most of the functions, except for groundwater recharge and litter quality. For communities with up to three or four planted species, groundwater recharge declined, whereas the water use efficiency of the ecosystem increased. If more than three or four species were planted, both functions remained stable. Nitrogen use was most efficient for monocultures. In contrast, litter quality increased with higher planted richness under current conditions reaching maximum quality for the most speciose community, while under future conditions litter quality declined with higher planted richness. Soil carbon increments and to a lower extent plant carbon increments were enhanced with higher planted richness, reaching their maximum at an intermediate richness, and remaining stable for higher values. Except for plant carbon increment, all ecosystem functions showed a decreasing spatial and temporal variability with increasing planted richness (Figure 2b; Figure S4.6).

3.2 | Trade-offs and synergies among ecosystem functions

With the eight plant species considered in this study, ecosystem multifunctionality could not fully be achieved, in current or future conditions (MF much smaller than 1, Figure 2a), since there are negative correlations (trade-offs) among functions (Figure 3a). Multifunctionality benefited from a strong positive correlation (synergy) between soil carbon increment and water use (Figures 2b and 3a). However, stronger trade-offs between ecosystem nitrogen use and litter quality as well as between groundwater recharge and ecosystem water use or soil carbon increment constrained the enhancement of the multifunctionality.

Most relationships between nitrogen use efficiency and other functions reversed under future conditions: in contrast to current conditions, an increase in nitrogen use efficiency was now accompanied by a decline in groundwater recharge as well as a strong increase in water use and soil carbon increment in the ecosystem. In addition, ecosystem litter quality and groundwater recharge could be increased at the same time under future conditions, which was not possible under current conditions. Some trade-offs and synergies observed under current conditions strengthened under the future climate scenario: trade-offs between ecosystem litter quality and ecosystem water usage, or soil carbon increment, became more apparent, whereas ecosystem nitrogen use efficiency and plant carbon increment were increased at the same time.

3.3 | Plant traits in the community and ecosystem functioning

Community-weighted mean plant traits could be linked to single ecosystem functions (Figure 3b). Particular trait combinations rather than single traits affected individual functions. Water- and nitrogen-related functions showed contrasting correlations to plant traits in the community, explaining their strong trade-offs. For example, under current conditions groundwater recharge (GWR) was enhanced by communities with a low SLA, higher investment into leaves than into roots (LM/RM), smaller crowns (maxCA), lower wood density (WD) and a higher wilting point (WP). In contrast, to achieve an improved ecosystem water use efficiency (EWU), wood density and maximum crown area should be larger in combination with a deeper rooting system (low value of rootL1). Very similar features that improved ecosystem water use efficiency also increased plant carbon increment (PCI) and soil carbon increment (SCI) in the ecosystem, supporting the synergies among the three functions.

Under future climatic conditions, correlations between functions and traits changed especially for soil carbon increment and water-related functions (Figure 3b). Traits associated with ecosystem

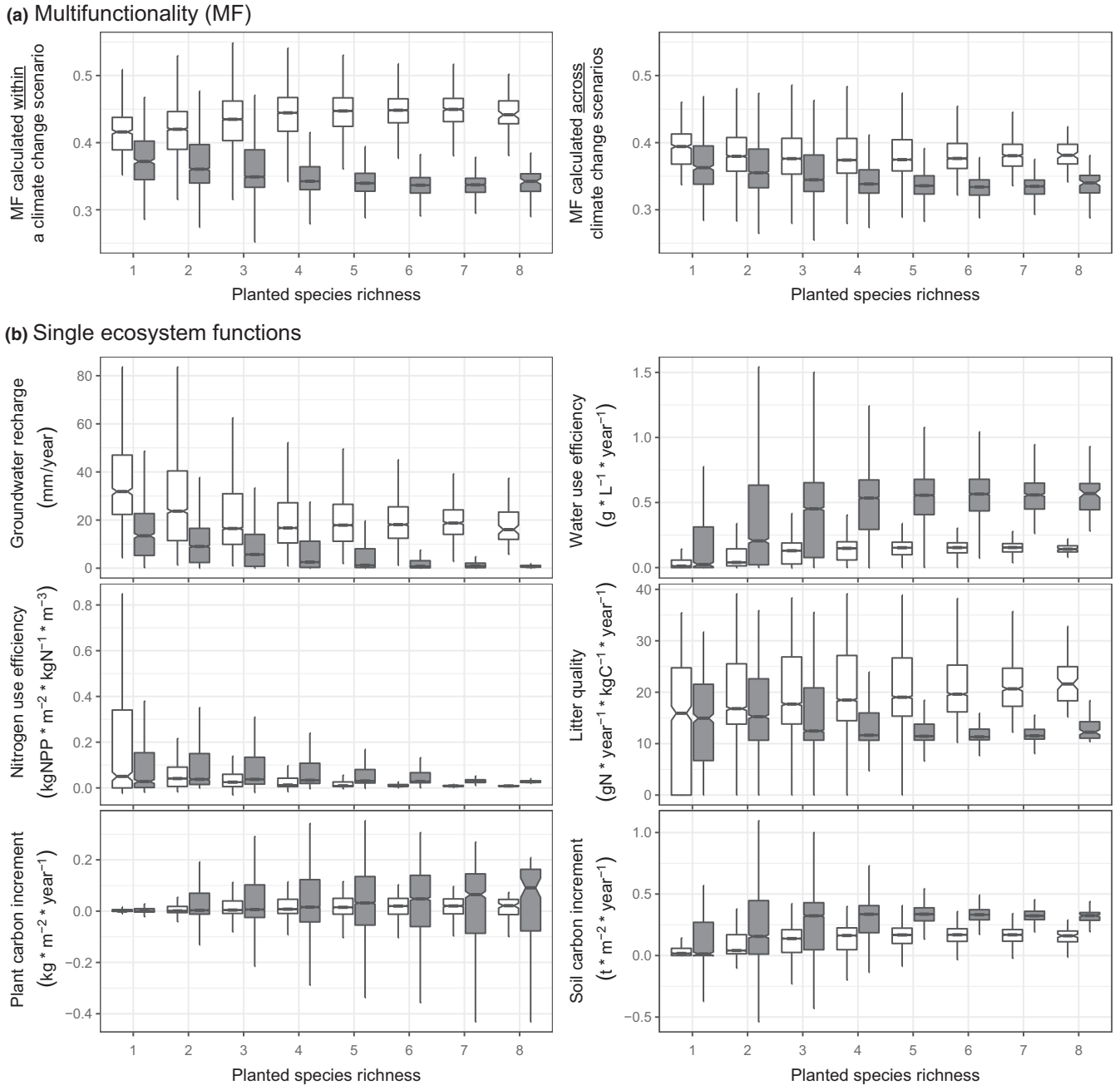

FIGURE 2 Multifunctionality (a) and single ecosystem functioning (b) for each planted species richness under current (white boxplots) and future climatic conditions (grey boxplots). Multifunctionality is either calculated within each climate scenario (a, left) or across climate scenarios (a, right). Shown is functioning for the last 10 simulated years and for 10 model repetitions as well as for 255 different plant communities which are unevenly distributed across the different planted species richness scenarios according to maximal possible combinations out of the pool of eight focal plant species. For better comparability among boxplots, single outliers are not shown

nitrogen use efficiency and litter quality showed no or limited change in importance. The underlying reason for these changes as well as the changes of the relationships among functions (Figure 3a) is that climate change affected functions differently: that is, either directly (e.g. Figure 4, changes in PCI not correlated with changes in SLA), indirectly via traits (e.g. Figure 4, changes in ELQ strongly correlated with changes in SLA) or by a combination of both (e.g. Figure 4, changes in GWR not correlated with changes in SLA but appearance of clusters of species compositions). For instance, the emerging trade-off between groundwater recharge and nitrogen use efficiency under climate warming (Figure 3a) was due to a negative direct and indirect effect of climate change on groundwater recharge as well as a slight positive and indirect effect of climate on nitrogen use efficiency (Figure 4).

In addition, we found that trait compositions shifted with climate change in particular for more speciose planted communities due to a loss of many species (Figures S4.1, S4.5 and S4.9), that is, shifts to plants with deeper roots, higher maximal crown area and with lighter

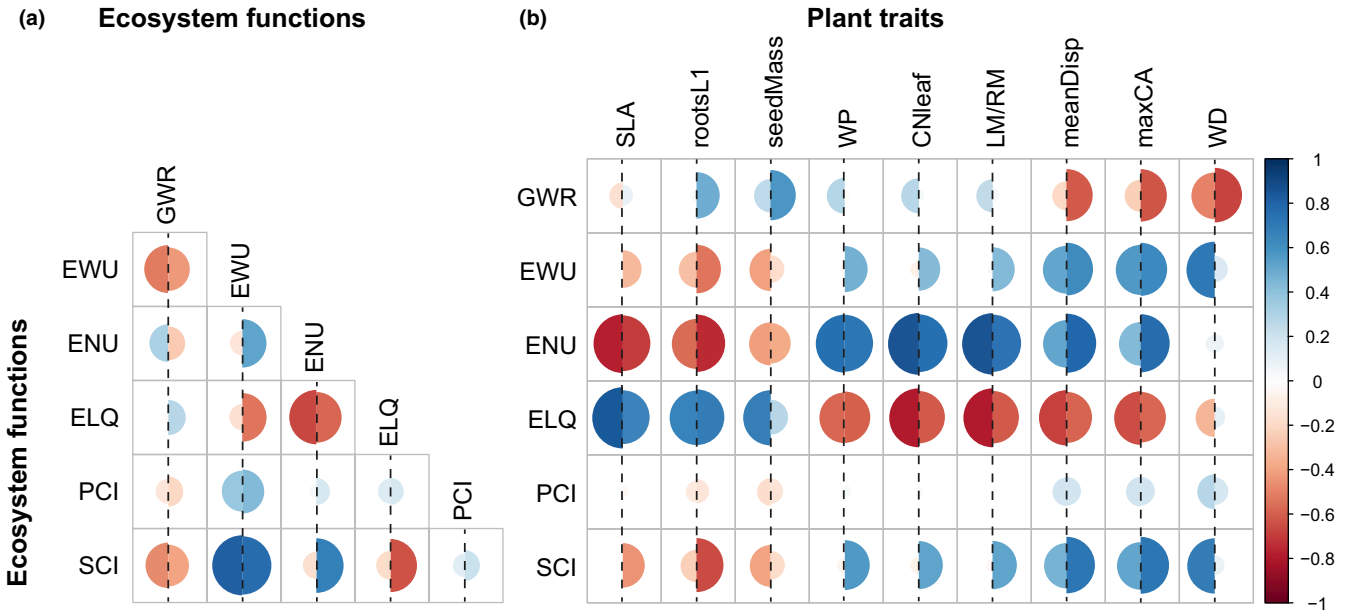

FIGURE 3 Negative (trade-off, red) and positive (synergy, blue) relationships among ecosystem functions (a) as well as between functions and community weighted mean (CWM) plant traits (b) under current (left half circle) and future climatic conditions (right half circle). Shown are significant Spearman's rank correlations ($\alpha = 0.05$) based on the last 10 simulated years and for 10 model repetitions across all 255 simulated plant communities. GWR, Groundwater recharge; EWU, Ecosystem water use efficiency; ENU, Ecosystem nitrogen use efficiency; ELQ, Ecosystem litter quality; PCI, Total plant carbon increment; SCI, Total soil carbon increment (see Table 1). Meaning of abbreviations for CWM plant traits can be found in Table 2

and far-dispersed seeds. These changes led to a larger reduction in groundwater recharge and ecosystem litter quality (Figures 2b and 3b), which explains the decreasing multifunctionality with increasing planted richness under climate change (Figure 2a).

4 | DISCUSSION

4.1 | Trade-offs among functions shift with climate change

As expected, we found that trade-offs prevented the achievement of restoration goals with simultaneous enhancement of multiple functions/services when the same trait or group of traits had positive effects on one function, but negative effects on a second function (e.g. de Bello et al., 2010; Teixeira et al., 2020). Instead, bundles of functions with synergies among them could be increased, and thus choice of the ecosystem services to be restored might be crucial. For instance, if managers want to improve water-efficient wood production and carbon sequestration [but not groundwater supply as also found by Cademus et al. (2014)], this can be achieved by planting communities with deeper roots, greater crown area and wood density as well as small seeds with larger dispersal distances.

We additionally found that trade-offs and synergies among ecosystem functions observed under current conditions shifted under future conditions, posing a clear challenge for long-term restoration where plant compositions are planted with the aim of delivering multiple ecosystem functions and services. We observed that these shifts in the relationships among functions can be explained either by a direct change of ecosystem functioning differently affected by changing environmental conditions and/or by an indirect change through uneven shifts in underlying community plant traits and thus changes in the correlations among CWM traits (cp. Zirbel et al., 2017). In our study, simulated climate change altered species and thus trait compositions as reviewed also by Maestre, Salguero-Gómez et al. (2012) for drylands as well as single trait–trait correlations as also shown by Ahrens et al. (2020). These climate change induced shifts resulted mostly through communities that for instance decreased groundwater recharge potentially via higher transpiration from the second soil layer and increased nitrogen use efficiency via less demand for nitrogen. At the same time, decrease in groundwater recharge was affected also directly by climate change via less available water for infiltration, and higher evapotranspiration due to warmer temperatures (cp. Reinecke et al., 2021). These uneven shifts mediated through different direct and indirect effects explain for instance the change from synergy to trade-off between groundwater recharge and nitrogen use efficiency. Therefore, the choice of specific plant species as well as changing environmental conditions should strongly be considered in restoration planning. Our modelling tool can facilitate this planning as it is able to simulate the short- and long-term effects of different plant species settings and environmental changes on ecosystem functioning. However, we note that we did consider only a limited pool of plant species and did not incorporate trait variation and plasticity, which might alone or in combination attenuate or enhance shifts in relationships among functions (Berzaghi et al., 2020; Liu & Ng, 2020).

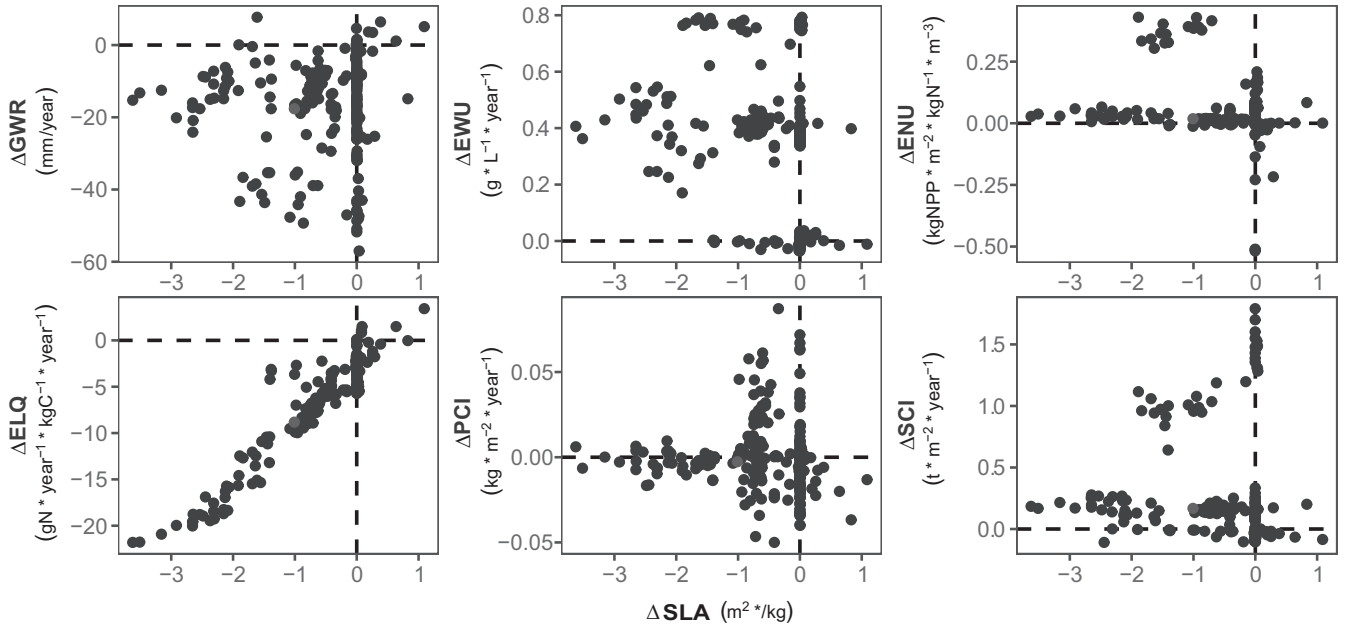

FIGURE 4 Disentangling direct and indirect effects of climate on ecosystem functioning by correlating climate change affected changes in CWM specific leaf area (ΔSLA) against changes in the six ecosystem functions. Shown are mean changes between current and future climatic conditions across the last 10 simulated years and 10 model repetitions per simulated plant community (black dots). Dashed lines separate plots into four quadrants with positive (top right) and negative (bottom left) changes in both trait and function; or trait and function differently affected (top left and bottom right). Values on dashed lines show no changes with climate change in functioning and/or trait. As we have strong trait–trait correlations that mostly remained the same under climate change (Figure S4.7), we only show the results for changes in CWM SLA (see Figure S4.8 for all traits). GWR, Groundwater recharge; EWU, Ecosystem water use efficiency; ENU, Ecosystem nitrogen use efficiency; ELQ, Ecosystem litter quality; PCI, Total plant carbon increment; SCI, Total soil carbon increment (see Table 1)

4.2 | Multifunctionality might not always be the right choice

If restoration aims to only increase ecosystem multifunctionality, we found that promoting plant diversity achieved this goal under current climatic condition, at least for our selected ecosystem functions as well as for our measure of multifunctionality. This is in line with previous findings and different measures of multifunctionality (Gross et al., 2017; Maestre, Quero, et al., 2012). However, our findings differed depending (a) on the choice of the multifunctionality measure (Figure S4.3, see also e.g. Byrnes et al., 2014, van der Plas, Manning, Allan, et al., 2016), (b) on the inclusion and weighting of certain functions (Figure S4.4, sell also e.g. Manning et al., 2018), as well as on the climatic context considered for the standardisation of the individual functions (Figure 2a, see also Giling et al., 2019). Therefore, if multifunctionality is the goal, these aspects should be well defined in collaboration with the stakeholders. For instance, if a certain minimum threshold of a function is desired, the level of the threshold can make a significant difference on the outcome (Figure S4.3). If the variability of a function is important, the multifunctionality measure as suggested by Maestre, Quero, et al. (2012) might be the choice, which in contrast to our chosen measure showed no clear relationship with increased species richness under current conditions, suggesting that variability strongly affected our results.

Furthermore, even though current multifunctionality in our study was improved by greater richness, single functions were differently impacted. For instance, ecosystem nitrogen use efficiency did not benefit from higher planted richness which contrasts empirical findings that have shown complementary effects of diverse woody plant communities on nitrogen use (e.g. Schwarz et al., 2014). Even though plant structural complementarity was considered in ModEST (see Appendix S1 e.g. eqn. 29), we focused on only eight evergreen woody species with similar C:N ratios (Table S2.1), of which only some survived (Figure S4.2), thus complementary nitrogen use was likely not prevalent. Other functions such as litter quality increased with planted richness under current conditions. This pattern is attributed to particular surviving species characterised by a high litter quality (Figure S4.9, low C:N in the leaves for more speciose planted combinations under current conditions).

In general, greater planted richness reduced spatial and temporal variability in ecosystem functioning (Figure S4.6), suggesting a more consistent supply across the species combinations planted. This could be due to functional redundancy acting as stabilising effect for a resilient supply of ecosystem functions (Mori et al., 2013). Under future conditions, however, higher plant diversity did not show greater resilience to environmental changes. Instead, we observed that with climate change speciose communities experienced greater species losses, potentially through higher interspecific competition (Ruiz-Benito et al., 2013), which in turn significantly lowered functional redundancy and thus the potential higher resilience against environmental changes. Also, even though multifunctionality

decreased with higher planted richness under future conditions, only single functions, that is, ecosystem litter quality, were largely affected and contributed to this decline, whereas most of the other functions increased with richness. Thus, the choice of metrics for restoration success should be considered if the goal is to improve a set of equally desired ecosystem functions and services at the same time.

4.3 | Applicability of our results for restoration world-wide

We successfully validated the process-based simulation model ModEST for a Mediterranean site in SW Australia and simulated the long-term effect of local plant choice on multifunctionality and six separate ecosystem functions related to water, nitrogen and carbon. We found that the ultimate aim to improve restoration outcomes with respect to improving multiple ecosystem functions at the same time under current and future climatic conditions was limited by trade-offs among ecosystem functions which shifted with climate change.

Even though we focused on a specific Mediterranean site with a focus on specific ecosystem functions, we believe that our general interpretations pertain to terrestrial systems globally. Underlying mechanisms driving trade-offs among functions and shifts in the trade-offs have been fundamentally shown across different ecosystems. For example, ecosystem functions are affected by underlying plant traits (e.g. de Bello et al., 2010; Funk et al., 2017) and environmental change either directly or indirectly, via changing plant trait compositions (e.g. De Deyn et al., 2008; Garnier et al., 2007). Thus, restoration ecologists across the world will face a clear challenge to achieve their targets under current conditions and in the long term.

With our validated model ModEST we were able to study the long-term coupled effects of various selected plant communities and climate change on ecosystem functioning. However, long-term functioning as well as trade-offs among functions should be further assessed by considering a wider range of inter- and intraspecific trait variability as well as further disturbances such as fire. We are aware that our findings are context dependent (e.g. dependent on local species pool, soil texture, weather and regional projected climate change) and thus differ across global ecosystems (e.g. Ding et al., 2020; Ratcliffe et al., 2017). In addition, since only bundles of services can be enhanced at the same time, different bundles could be integrated across the landscape to achieve landscape multifunctionality (Lovell & Johnston, 2009; van der Plas, Manning, Soliveres, et al., 2016; van der Plas et al., 2019). These units with their abiotic and biotic characteristics could be simulated individually with ModEST but evaluated at the same time to assess how individual units should be restored to achieve landscape-scale targets. Furthermore, various ecosystems are degraded differently, and therefore restoration managers need to improve different desired functions and services.

4.4 | Bringing ModEST into practice

With this study we applied the steps suggested by Fiedler et al. (2018) in order to improve ecological restoration and showed that models like ModEST can serve as a planning tool to better understand the suite of desired ecosystem functions and services that can be restored in any particular place based on the plant species available and the local environmental conditions. When restoration with respect to improving the long-term provision of ecosystem functions/services by planting woody plants is the goal, we suggest the following steps.

First, define desired ecosystem functions/services, their weightings and the environmental context of interest (e.g. ecosystem under current, future or both climatic conditions) for the standardisation of the individual ecosystem functions. If threshold multifunctionality approach is of interest define the minimum desired threshold of functioning. Next, choose the potential plant species pool for the restoration of the site. Even though we focused on only biophysical ecosystem functions, they can be directly linked to several ecosystem services (see Table 1), which might be of greater applicability for particular restoration projects. Other ecosystem services that are not directly modelled can be indirectly estimated from additional plant characteristics of the simulated communities via known relationships between these characteristics and services. For instance, pollination is not modelled in ModEST but could be estimated from flower traits that are known for the species simulated. Species selection and the specific restoration goals and how they are measured from the model should be determined in collaboration with stakeholders.

Second, parameterise ModEST for the environmental conditions of the restoration site as well as for the selected plant species. The individual-based ecosystem model ModEST links ubiquitous processes related to hydrology, nitrogen and carbon cycling to local abiotic and biotic conditions, and therefore allows for applying the model to various terrestrial ecosystems on Earth. If enough data are available, validate the model for the site and the chosen species. Subsequently, run ModEST scenarios with all potential or selected plant combinations in a full-factorial design with climate change scenarios.

Last, analyse model outcomes and recommend plant compositions that meet restoration goals best under current and/or future conditions.

ACKNOWLEDGEMENTS

This work was supported by the German Research Foundation (DFG project TI 824/3-1), the German Academic Exchange Service, and the University Alliance for Sustainability. The set-up of Ridgefield was supported by an Australian Research Council Laureate Fellowship to Richard J. Hobbs and funding from The University of Western Australia; UWA and the ARC Centre of Excellence for Environmental Decisions provide continued support. M.P.P. was supported by the European Research Council PASTFORWARD project, awarded to Kris Verheyen (ERC Consolidator Grant 614839). The authors thank the HPC Service of ZEDAT at Freie Universität Berlin (Bennett

et al., 2020) for computing time, Marie-Sophie Rohwäder and Jonas Roth for data processing, Florian Hartig for his support on the Bayesian R package, three anonymous reviewers, Lars Brudvig, Selina Baldauf, Katja Irob and Felix Wesener for their constructive feedback on the manuscript as well as Rebecca Campbell and Tim Morald for their support regarding the Ridgefield experiment.

AUTHORS' CONTRIBUTIONS

S.F., M.P.P. and B.T. conceived the project; S.F. implemented the hydrological and plant module, parameterised ModEST, conducted the experiments, analysed the simulation outcomes, prepared all figures and tables and wrote the first draft of the manuscript in close collaboration with B.T. and M.P.P.; J.A.F.M. implemented the nutrient module; K.B.H., M.P.P. and R.J.S. participated in the conception and implementation of the Ridgefield experiment. All authors interpreted data, contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The source code of ModEST available from GitHub https://doi.org/10.5281/ZENODO.4034790 (Fiedler et al., 2020). Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.dr7sqv9z0 (Fiedler et al., 2021).

ORCID

Sebastian Fiedler https://orcid.org/0000-0001-5620-6989
José A. F. Monteiro https://orcid.org/0000-0002-3520-9918
Kristin B. Hulvey https://orcid.org/0000-0001-9062-4113
Rachel J. Standish https://orcid.org/0000-0001-8118-1904
Michael P. Perring https://orcid.org/0000-0001-8553-4893
Britta Tietjen https://orcid.org/0000-0003-4767-6406

REFERENCES

Ahrens, C. W., Andrew, M. E., Mazanec, R. A., Ruthrof, K. X., Challis, A., Hardy, G., Byrne, M., Tissue, D. T., & Rymer, P. D. (2020). Plant functional traits differ in adaptability and are predicted to be differentially affected by climate change. *Ecology and Evolution*, *10*, 232–248. https://doi.org/10.1002/ece3.5890

Bennett, E. M., Peterson, G. D., & Gordon, L. J. (2009). Understanding relationships among multiple ecosystem services. *Ecology Letters*, *12*, 1394–1404. https://doi.org/10.1111/j.1461-0248.2009.01387.x

Bennett, L., Melchers, B., & Proppe, B. (2020). *Curta: A general-purpose high-performance computer at ZEDAT*. Freie Universität Berlin. https://doi.org/10.17169/refubium-26754

Berzaghi, F., Wright, I. J., Kramer, K., Oddou-Muratorio, S., Bohn, F. J., Reyer, C. P. O., Sabaté, S., Sanders, T. G. M., & Hartig, F. (2020). Towards a new generation of trait-flexible vegetation models. *Trends in Ecology & Evolution*, *35*, 191–205. https://doi.org/10.1016/j.tree.2019.11.006

Bureau of Meteorology. (2019). http://www.bom.gov.au/

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J., Hooper, D. U., Dee, L. E., & Emmett Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, *5*, 111–124. https://doi.org/10.1111/2041-210X.12143

Cademus, R., Escobedo, F. J., McLaughlin, D., & Abd-Elrahman, A. (2014). Analyzing trade-offs, synergies, and drivers among timber production, carbon sequestration, and water yield in pinus elliotii forests in southeastern USA. *Forests*, *5*(6), 1409–1431. https://doi.org/10.3390/f5061409

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67. https://doi.org/10.1038/nature11148

Cowling, R. M., Rundel, P. W., Lamont, B. B., Arroyo, M. K., & Arianoutsou, M. (1996). Plant diversity in mediterranean-climate regions. *Trends in Ecology & Evolution*, *11*, 362–366. https://doi.org/10.1016/0169-5347(96)10044-6

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., Berg, M. P., Cipriotti, P., Feld, C. K., Hering, D., Martins da Silva, P., Potts, S. G., Sandin, L., Sousa, J. P., Storkey, J., Wardle, D. A., & Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, *19*, 2873–2893. https://doi.org/10.1007/s10531-010-9850-9

De Deyn, G. B., Cornelissen, J. H. C., & Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, *11*, 516–531. https://doi.org/10.1111/j.1461-0248.2008.01164.x

DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000Prime Reports*, *6*. https://doi.org/10.12703/P6-39

Ding, J., Travers, S. K., Delgado-Baquerizo, M., & Eldridge, D. J. (2020). Multiple trade-offs regulate the effects of woody plant removal on biodiversity and ecosystem functions in global rangelands. *Global Change Biology*, *26*, 709–720. https://doi.org/10.1111/gcb.14839

Esther, A., Groeneveld, J., Enright, N. J., Miller, B. P., Lamont, B. B., Perry, G. L. W., Tietjen, B., & Jeltsch, F. (2011). Low-dimensional trade-offs fail to explain richness and structure in species-rich plant communities. *Theoretical Ecology*, *4*, 495–511. https://doi.org/10.1007/s12080-010-0092-y

Fiedler, S., Monteiro, J. A. F., Hulvey, K. B., Standish, R. J., Perring, M. P., & Tietjen, B. (2021). Data from: Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.dr7sqv9z0

Fiedler, S., Monteiro, J. A. F., Perring, M. P., & Tietjen, B. (2020). ModEST v1.0: Modelling ecosystem functions and services based on traits. https://doi.org/10.5281/ZENODO.4034790

Fiedler, S., Perring, M. P., & Tietjen, B. (2018). Integrating trait-based empirical and modeling research to improve ecological restoration. *Ecology and Evolution*, *8*, 6369–6380. https://doi.org/10.1002/ece3.4043

Fu, B., Wang, S., Su, C., & Forsius, M. (2013). Linking ecosystem processes and ecosystem services. *Current Opinion in Environmental Sustainability*, *5*, 4–10. https://doi.org/10.1016/j.cosust.2012.12.002

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., Laughlin, D. C., Sutton-Grier, A. E., Williams, L., & Wright, J. (2017). Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews*, *92*, 1156–1173. https://doi.org/10.1111/brv.12275

Fyllas, N. M., & Troumbis, A. Y. (2009). Simulating vegetation shifts in north-eastern Mediterranean mountain forests under climatic change scenarios. *Global Ecology and Biogeography*, *18*, 64–77. https://doi.org/10.1111/j.1466-8238.2008.00419.x

Gamfeldt, L., & Roger, F. (2017). Revisiting the biodiversity–ecosystem multifunctionality relationship. *Nature Ecology & Evolution*, *1*, 1–7. https://doi.org/10.1038/s41559-017-0168

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology*, *27*(S1). https://doi.org/10.1111/rec.13035

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., … Zarovali, M. P. (2007). Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, *99*, 967–985. https://doi.org/10.1093/aob/mcl215

Giling, D. P., Beaumelle, L., Phillips, H. R. P., Cesarz, S., Eisenhauer, N., Ferlian, O., Gottschall, F., Guerra, C., Hines, J., Sendek, A., Siebert, J., Thakur, M. P., & Barnes, A. D. (2019). A niche for ecosystem multifunctionality in global change research. *Global Change Biology*, *25*, 763–774. https://doi.org/10.1111/gcb.14528

Gross, N., Bagousse-Pinguet, Y. L., Liancourt, P., Berdugo, M., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology & Evolution*, *1*, 1–9. https://doi.org/10.1038/s41559-017-0132

Hope, P., Abbs, D., Bhend, J., Chiew, F., Church, J., Ekström, M., Kirono, D., Lenton, A., Lucas, C., McInnes, K., Moise, A., Monselesan, D., Mpelasoka, F., Timbal, B., Webb, L., & Whetton, P. (2015). Southern and south-western flatlands cluster report, climate change in Australia projections for Australia's natural resource management regions: Cluster reports. CSIRO and Bureau of Meteorology. (pp. 1–64).

IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat.

IPCC. (2014). *Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate*. IPCC.

Kemanian, A. R., Julich, S., Manoranjan, V. S., & Arnold, J. R. (2011). Integrating soil carbon cycling with that of nitrogen and phosphorus in the watershed model SWAT: Theory and model testing. *Ecological Modelling*, *222*, 1913–1921. https://doi.org/10.1016/j.ecolmodel.2011.03.017

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, *17*, 771–784. https://doi.org/10.1111/ele.12288

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Leakey, A. D. B., Ainsworth, E. A., Bernacchi, C. J., Rogers, A., Long, S. P., & Ort, D. R. (2009). Elevated CO_2 effects on plant carbon, nitrogen, and water relations: Six important lessons from FACE. *Journal of Experimental Botany*, *60*(10), 2859–2876. https://doi.org/10.1093/jxb/erp096

Liu, S., & Ng, G.-H. C. (2020). The role of spatiotemporal plant trait variability in model predictions of ecohydrological responses to climate change in a desert shrubland. *Journal of Hydrology*, *588*, 125088. https://doi.org/10.1016/j.jhydrol.2020.125088

Lovell, S. T., & Johnston, D. M. (2009). Creating multifunctional landscapes: How can the field of ecology inform the design of the landscape? *Frontiers in Ecology and the Environment*, *7*, 212–220. https://doi.org/10.1890/070178

Luo, Y., El-Madany, T., Ma, X., Nair, R., Jung, M., Weber, U., Filippa, G., Bucher, S. F., Moreno, G., Cremonese, E., Carrara, A., Gonzalez-Cascon, R., Cáceres Escudero, Y., Galvagno, M., Pacheco-Labrador, J., Martín, M. P., Perez-Priego, O., Reichstein, M., Richardson, A. D., … Migliavacca, M. (2020). Nutrients and water availability constrain the seasonality of vegetation activity in a Mediterranean ecosystem. *Global Change Biology*, *26*, 4379–4400. https://doi.org/10.1111/gcb.15138

Luo, Y., Gerten, D., Le Maire, G., Parton, W. J., Weng, E., Zhou, X., Keough, C., Beier, C., Ciais, P., Cramer, W., Dukes, J. S., Emmett, B., Hanson, P. J., Knapp, A., Linder, S., Nepstad, D., & Rustad, L. (2008). Modeled interactive effects of precipitation, temperature, and [CO_2] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, *14*(9), 1986–1999. https://doi.org/10.1111/j.1365-2486.2008.01629.x

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M., Bowker, M. A., Soliveres, S., Escolar, C., Garcia-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., … Zaady, E. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, *335*(6065), 214–218. https://doi.org/10.1126/science.1215442

Maestre, F. T., Salguero-Gómez, R., & Quero, J. L. (2012). It is getting hotter in here: Determining and projecting the impacts of global environmental change on drylands. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 3062–3075. https://doi.org/10.1098/rstb.2011.0323

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., Whittingham, M. J., & Fischer, M. (2018). Redefining ecosystem multifunctionality. *Nature Ecology & Evolution*, *2*, 427–436. https://doi.org/10.1038/s41559-017-0461-7

May, F., Grimm, V., & Jeltsch, F. (2009). Reversed effects of grazing on plant diversity: The role of below-ground competition and size symmetry. *Oikos*, *118*, 1830–1843. https://doi.org/10.1111/j.1600-0706.2009.17724.x

Meyer, S. T., Ptacnik, R., Hillebrand, H., Bessler, H., Buchmann, N., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Halle, S., Klein, A.-M., Oelmann, Y., Roscher, C., Rottstock, T., Scherber, C., Scheu, S., Schmid, B., Schulze, E.-D., Temperton, V. M., … Weisser, W. W. (2018). Biodiversity-multifunctionality relationships depend on identity and number of measured functions. *Nature Ecology & Evolution*, *2*, 44–49. https://doi.org/10.1038/s41559-017-0391-4

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, *88*, 349–364. https://doi.org/10.1111/brv.12004

Pacala, S. W., & Deutschman, D. H. (1995). Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos*, *74*, 357. https://doi.org/10.2307/3545980

Perring, M. P., Standish, R. J., Hulvey, K. B., Lach, L., Morald, T. K., Parsons, R., Didham, R. K., & Hobbs, R. J. (2012). The ridgefield multiple ecosystem services experiment: Can restoration of former agricultural land achieve multiple outcomes? *Agriculture, Ecosystems & Environment*, *163*, 14–27. https://doi.org/10.1016/j.agee.2012.02.016

Perring, M. P., Standish, R. J., Price, J. N., Craig, M. D., Erickson, T. E., Ruthrof, K. X., Whiteley, A. S., Valentine, L. E., & Hobbs, R. J. (2015). Advances in restoration ecology: Rising to the challenges of the coming decades. *Ecosphere*, *6*, art131. https://doi.org/10.1890/ES15-00121.1

Plas, F., Allan, E., Fischer, M., Alt, F., Arndt, H., Binkenstein, J., Blaser, S., Blüthgen, N., Böhm, S., Hölzel, N., Klaus, V. H., Kleinebecker, T., Morris, K., Oelmann, Y., Prati, D., Renner, S. C., Rillig, M. C., Schaefer, H. M., Schloter, M., … Manning, P. (2019). Towards the development of general rules describing landscape heterogeneity–multifunctionality relationships. *Journal of Applied Ecology*, *56*, 168–179. https://doi.org/10.1111/1365-2664.13260

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., … Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, *20*, 1414–1426. https://doi.org/10.1111/ele.12849

Reinecke, R., Müller Schmied, H., Trautmann, T., Andersen, L. S., Burek, P., Flörke, M., Gosling, S., Grillakis, M., Hanasaki, N., Koutroulis, A., Pokhrel, Y., Thiery, W., Wada, Y., Yusuke, S., & Döll, P. (2021).

Uncertainty of simulated groundwater recharge at different global warming levels: A global-scale multi-model ensemble study. *Hydrology and Earth System Sciences*, *25*(2), 787–810. https://doi.org/10.5194/hess-25-787-2021

Ruiz-Benito, P., Lines, E. R., Gómez-Aparicio, L., Zavala, M. A., & Coomes, D. A. (2013). Patterns and drivers of tree mortality in Iberian forests: Climatic effects are modified by competition. *PLoS ONE*, *8*, https://doi.org/10.1371/journal.pone.0056843

Sala, O. E. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Schaphoff, S., von Bloh, W., Rammig, A., Thonicke, K., Biemans, H., Forkel, M., Gerten, D., Heinke, J., Jägermeyr, J., Knauer, J., Langerwisch, F., Lucht, W., Müller, C., Rolinski, S., & Waha, K. (2018). LPJmL4 – a dynamic global vegetation model with managed land – Part 1: Model description. *Geoscientific Model Development*, *11*(4), 1343–1375. https://doi.org/10.5194/gmd-11-1343-2018

Schwarz, M. T., Bischoff, S., Blaser, S., Boch, S., Schmitt, B., Thieme, L., Fischer, M., Michalzik, B., Schulze, E.-D., Siemens, J., & Wilcke, W. (2014). More efficient aboveground nitrogen use in more diverse Central European forest canopies. *Forest Ecology and Management*, *313*, 274–282. https://doi.org/10.1016/j.foreco.2013.11.021

Shackelford, N., Hobbs, R. J., Burgar, J. M., Erickson, T. E., Fontaine, J. B., Laliberté, E., Ramalho, C. E., Perring, M. P., & Standish, R. J. (2013). Primed for change: Developing ecological restoration for the 21st century. *Restoration Ecology*, *21*, 297–304. https://doi.org/10.1111/rec.12012

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., & Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*, 161–185. https://doi.org/10.1046/j.1365-2486.2003.00569.x

Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences*, *11*(7), 2027–2054. https://doi.org/10.5194/bg-11-2027-2014

Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M., Renner, S. C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Buscot, F., Diekötter, T., Heinze, J., … Allan, E. (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature*, *536*(7617), 456–459. https://doi.org/10.1038/nature19092

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jckson, S. T., & Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*, 1125–1140.

Teixeira, L. H., Oliveira, B. F., Krah, F. S., Kollmann, J., & Ganade, G. (2020). Linking plant traits to multiple soil functions in semi-arid ecosystems. *Journal of Arid Environments*, *172*, 104040. https://doi.org/10.1016/j.jaridenv.2019.104040

Tietjen, B., Zehe, E., & Jeltsch, F. (2009). Simulating plant water availability in dry lands under climate change: A generic model of two soil layers. *Water Resources Research*, *45*(1), https://doi.org/10.1029/2007wr006589

van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., … Fischer, M. (2016). Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nature Communications*, *7*(1), https://doi.org/10.1038/ncomms11109

van der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., … Fischer, M. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences*, *113*(13), 3557–3562. https://doi.org/10.1073/pnas.1517903113

Zirbel, C. R., Bassett, T., Grman, E., & Brudvig, L. A. (2017). Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *Journal of Applied Ecology*, *54*, 1070–1079. https://doi.org/10.1111/1365-2664.12885

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Fiedler S, Monteiro JAF, Hulvey KB, Standish RJ, Perring MP, Tietjen B. Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. *J Appl Ecol*. 2021;00:1–13. https://doi.org/10.1111/1365-2664.13900